SURVIVAL AND CAUSES OF MORTALITY IN WINTERING SHARP-SHINNED HAWKS AND COOPER'S HAWKS

TIMOTHY C. ROTH, II,^{1,3} STEVEN L. LIMA,¹ AND WILLIAM E. VETTER^{1,2}

ABSTRACT.—Sharp-shinned Hawks (*Accipiter striatus*) and Cooper's Hawks (*A. cooperii*) are important predators of birds in North America, but little is known about their natural history during the winter. Even basic survival information is not well documented in these species and is generally unknown during the winter. Therefore, we examined survivorship and causes of mortality among wintering Cooper's and Sharp-shinned hawks. We radio-tracked 27 Cooper's and 40 Sharp-shinned hawks during 5 winters from 1999 to 2004. Neither species nor sex was a significant covariate of survivorship, but the probability of adult survival (75.4%) over 110 days was significantly higher than that of juveniles (9.4%). Our estimate of adult survivorship is comparable with those published for other accipiters, but our estimate for juveniles is lower. Age differences in survivorship may be attributed to risk taking or inexperience in juveniles and/or difficulties in dealing with transmitter attachments. Two types of mortality (predation and collisions) were observed in the study. Whereas predation by owls was a major source of mortality in rural habitat, no predation was observed in the urban habitat. Our results suggest that predation by owls may have important implications for the behavioral interactions between accipiters and their prey. *Received 20 October 2004, accepted 31 May 2005.*

Although Sharp-shinned Hawks (Accipiter striatus) and Cooper's Hawks (A. cooperii) are the main predators of small birds wintering in North America, very little is known about their natural history during the winter. Even basic information, such as diet, hunting patterns, general movements, and home-range size, is lacking (Rosenfield and Bielefeldt 1993, Bildstein and Meyer 2000). This lack of information is particularly problematic given that these hawks play a critical role in an important conceptual paradigm in behavioral ecology: the small-bird-in-winter. Under this paradigm, small birds face trade-offs between the risks of starvation and predation from accipiter hawks. This conceptual paradigm has had great impact on our present understanding of many aspects of behavioral ecology, such as sociality (Pulliam and Caraco 1984, Boinski and Garber 2000), foraging behavior (Lima 1985, Stephens and Krebs 1986), and predator-prey theory (Mangel and Clark 1988, Houston and McNamara 1999).

Like other aspects of their natural history, the demography of Sharp-shinned and Cooper's hawks is poorly understood (Rosenfield

and Bielefeldt 1993, Bildstein and Meyer 2000). Basic survivorship estimates and the relative importance of causes of mortality are unknown during winter and rarely documented during the rest of the year. Much of what we know about accipiter survival is based on banding data (see Keran 1981). For Cooper's Hawks, survivorship estimates from band recoveries are 19-28% for first-year birds and 63-79% for older birds (Henny and Wight 1972, Boal 1997). Some recent telemetry information from breeding studies of Cooper's Hawks in urban sites resulted in survivorship estimates of 49% for nestlings (Boal and Mannan 1999) and 67% from post-fledgling to midwinter (Mannan et al. 2004), but no other estimates of survivorship have been published for adults. Similarly, limited band recoveries published by Palmer (1988) resulted in survivorship estimates of 20-25% for Sharpshinned Hawks. To our knowledge, there are no other published data on the survivorship of these two species.

Although relatively little information exists on Cooper's Hawks and Sharp-shinned Hawks, perhaps the best available insights into their survival rates come from studies of other accipiters. In North America, Northern Goshawk (*A. gentilis*) survivorship is estimated at 33% for first-year birds, 68% for subadults, and 81% for adults (Squires and Reynolds 1997). Dewey and Kennedy (2001) estimated a greater average first-year survivorship

¹ Dept. of Ecology and Organismal Biology, Indiana State Univ., Terre Haute, IN 47809, USA.

² Current address: Thunderbird Wildlife Consulting, Inc., 1901 Energy Ct., Ste. 115, Gillette, WY 82718, USA.

³ Corresponding author; e-mail: lsroth@isugw. indstate.edu

(control group only, 73%), similar to that estimated for sub-adults by Squires and Reynolds (1997). Another source of information on accipiter survivorship comes from European studies of the goshawk and the Eurasian Sparrowhawk (A. nisus). Tornberg and Colpaert (2001) estimated goshawk survivorship at 43% for first-year birds, and about 84% in older birds. Kenward et al. (1999) estimated similar rates of survival at approximately 50% for first-year males, 70% for first-year females, and about 80% for both sexes in older birds. While juvenile survivorship is considerably lower in sparrowhawks (30% for males, 50% for females) than in goshawks, adult survival rates are comparable at nearly 70% for both sexes of both species (Newton 1975; Newton et al. 1983, 1999). Based on the information available for other accipiters, the general pattern seems to be that juvenile survival is approximately half that of adults.

Little consideration has been given to the causes of mortality in post-fledgling Sharpshinned and Cooper's hawks. Based on the scant information that exists, human-induced mortality seems to be due mainly to collisions with windows or automobiles (Keran 1981, Klem 1990, Klem et al. 2004) and electrocution (Lehman 2001). Similarly, Boal (1997) attributed 68% of adult Cooper's Hawk mortality to collisions with automobiles or windows, and 3% to electrocution. As urban populations of accipiters (especially Cooper's Hawk) increase, such "accidental" mortality may become increasingly common (see Boal and Mannan 1999). Mortality due to gunshot and poison (important causes of mortality in the past) have greatly diminished since implementation of federal protection and the elimination of DDT/DDE in North America (Keran 1981), although Boal (1997) reports recent mortality rates from gunshot (13%) and poison (6%) for Cooper's Hawks. Natural predation by owls and other raptors on accipiters has been documented (Klem et al. 1985, George 1989), but the demographic importance of such predation is unknown. Disease may also be an important mortality factor, particularly during the breeding season (Ward and Kennedy 1996, Boal et al. 1998).

The objective of our research was to obtain a better understanding of accipiter natural history and behavior, with the long-term goal of obtaining insight into predator-prey interactions in wintering birds. We studied the behavior and general natural history of Cooper's and Sharp-shinned hawks over several winter periods. Here, we present data on one aspect of accipiter natural history: winter survival and causes of mortality. As little is known about North American accipiters, predictions are difficult; however, our expectation was that Sharp-shinned Hawks were more likely targets of predation due to their smaller size. which may result in lower survival relative to that of Cooper's Hawks. Based on studies of other accipiters, we also expected juvenile mortality of Cooper's and Sharp-shinned hawks to be greater than that of adults.

METHODS

Study site.-Our study site was centered in Vigo County in west-central Indiana and the adjacent counties in Indiana and eastern Illinois. The site included both urban and rural areas. Our urban area was centered at Terre Haute, Indiana (pop. 60,000; 39° 27.1' N, 87° 18.5' W) and covered approximately 40 km². There, we focused on Cooper's Hawks, mainly during the winter seasons of 1999-2001 (see also Roth and Lima 2003); one Cooper's Hawk was also tracked into the urban site during the winter of 2003-2004. Approximately 30% of this area consisted of high-density residential and commercial properties (>14 buildings/block), whereas the remaining 70% encompassed lower-density residential areas (<14 buildings/block; Topologically Integrated Geographic Encoding and Referencing [TI-GER] data, U.S. Census Bureau, Geography Division 2000, http://www.census.gov/geo/ www/tiger/). Although we attempted to study Sharp-shinned Hawks in this urban setting, none could be trapped and few were observed.

Our rural area included all areas adjacent to, and mainly west of, the Wabash River, which is to the immediate southwest of our urban area. Here, we focused mainly on Sharp-shinned Hawks during the winter seasons of 2000–2004, but also tracked several Cooper's Hawks. Northern Goshawks were not included in this study, as they are very rare in west-central Indiana; only one was observed during the 5-year study, and only one has been recorded during the 45 years of the local Christmas Bird Count (P. E. Scott pers. comm.). The rural study area covered approximately 1,000 km² and included small clusters of houses, agricultural land, and fragmented forest. The landscape was composed of approximately 3.7% residential, 48% agricultural field (bare in winter), 17.9% grass/fallow field, 24.9% upland forest, 3.7% bottomland forest, 0.4% wetland, and 1.4% water (lakes, ponds, river).

Capture and tracking.-Using constantly monitored bal-chatri traps (Berger and Mueller 1959) and bow nets, we conducted trapping from late November through late January during each winter. Traps were baited with European Starlings (Sturnus vulgaris) and House Sparrows (Passer domesticus). We positioned traps in open areas, along potential travel paths, and at potential roost locations used by accipiters. For example, in the city, we commonly trapped in parking lots, cemeteries, and recreational parks, and, in the rural area, we trapped in bare fields, along roadsides and power lines, and at a few long-established bird feeders. We recaptured only one individual during the study, whereupon we removed the transmitter and harness and examined the hawk for signs of transmitter-related stress. Once captured, our accipiters assiduously avoided traps on future encounters (TCR and SLL pers. obs.).

We used radio-telemetry to track hawks. Hawks were fitted with 2.4- to 11.0-g position-sensitive transmitters (models BD-2P, PD-2P, and RI-2CP; Holohil Systems, Carp, Ontario, Canada; Sharp-shinned Hawks: male, 2.4 g; female, 3.5-4.5 g; Cooper's Hawks: male, 4.2-5.8 g; female, 6.9-11.0 g) using the pelvic harness technique of Rappole and Tipton (1994; see also Roth and Lima 2003). In all cases, transmitter mass was <3% (mean = $2.09\% \pm 0.09$ SE) of the hawk's total body mass. Transmitters had a life expectancy of approximately 3 months (2.4-g model) to over 6 months (11.0-g model). A position-sensitive switch on the transmitters provided information on hawk posture (horizontal or vertical) and was instrumental in determining mortality. A stationary signal indicating that the transmitter was horizontal-with no fluctuation-was usually a good indication of mortality, which prompted attempts to conduct visual verification.

Tracking was usually conducted from the

day of capture until the hawk was found dead or had abandoned the study site, or until the transmitter failed. All hawks were tracked ≥ 2 hr (frequently up to 10 hr) daily from vehicles using yagi and whip antennae. In addition, activity was monitored at roosts 0.5 to 1 hr before sunrise and 0.5 to 1 hr after sunset. The primary purpose of this intensive tracking was to collect detailed behavioral data, such as diet, movement, and activity. Due to this intensive tracking, we are certain of the day during which a hawk died or left the study site. If a hawk's signal was lost, we verified its departure with systematic scanning of the entire study site for \geq 7 days. We distinguished hawk departure from transmitter failure in two ways: (1) transmitters that were about to fail typically produced signature shifts in signal (C. J. Amlaner pers. comm.), and (2) transmitters lost due to harness failure were retrieved. The hawks did not demonstrate any evidence of disturbance by our presence in vehicles, so we assumed that our tracking did not provoke any movement from the site.

Sources of mortality were predation and accidents (collisions with windows and vehicles). Although we did not observe predation events, we used the condition of the kill to determine the probable cause of predator-induced mortality. Plucked remains in a neat pile suggested predation by an accipiter, most likely Cooper's Hawk (TCR and SLL pers. obs.), whereas remains that were mostly intact, but decapitated or cleanly cut in half (Houston et al. 1998, Mazur and James 2000) with large, triangular incisions, and/or those with crimped antenna, suggested owl predation. In most cases, we were able to recover the carcass within 12 hr of death (i.e., early the next morning when the hawk did not leave roost). We usually recovered the posterior portion of the carcass, as the transmitters were never removed from the body. All retrieved carcasses of hawks that had died during the night showed signs of predation; none had conical teeth marks or masticated bones. This is strong evidence that hawks were not scavenged by mammals during the night, but were killed on or near their roost by owls.

For deaths from collision, we used the location and condition of the carcass to identify the object with which the hawk collided. Remains found along a roadside with signs of blunt trauma, but with no sign of predation, were considered vehicular-collision mortalities, whereas those found near a house and with no sign of predation, but with apparent trauma to the head, were considered windowcollision mortalities. Although we observed some hawks collide with windows, none of the observed cases resulted in mortality. If we could not recover the remains within 1 day, we used the location of the kill to determine the probable cause of mortality (predation versus collision near house). If the location provided no clear indication of the cause of mortality, the cause was considered unknown.

Survivorship analysis.-We estimated survivorship using the Kaplan-Meier procedure (Kaplan and Meier 1958) with a Cox proportional hazard regression model (Cox 1972) to determine the effects of sex, age, and species on survival using Systat (SPSS, Inc. 1998). The Cox model produces a standard survivor function and permits the analysis of covariates with proportional shifts of the hazard function. We used sex and species as covariates of survival and stratified by age to distinguish differences between juveniles (hawks in their first year) and adults (hawks after their first year). A log-rank Mantel test was used to reveal differences between the age strata (SPSS, Inc. 1998). All data points were right censored when hawks left the study site as itinerants (birds lacking stable home ranges and possibly still migrating) or migrants (birds that moved north in March or April), or were lost for other reasons (e.g., transmitter failure). We do not include hawks depredated within 7 days of transmitter attachment (four cases), as these deaths were possibly related to capture, the transmitter, or the transmitter attachment and are possibly the result of preoccupation with the transmitter and the resulting lack of vigilance. In all hawks, transmitter "grooming" was minimal by the 2nd or 3rd full day of transmitter attachment; thus, the 7-day period was thought to be long enough to remove the effects of newly attached transmitters from the analysis.

RESULTS

We captured and tracked 40 Sharp-shinned Hawks (40 rural, 0 urban) and 27 Cooper's Hawks (14 rural, 13 urban) during the 5-winter study. The sex ratio of captured hawks was not significantly different from 1:1 for either species (Sharp-shinned Hawks: males = 18, females = 22, $\chi^2 = 0.40$, df = 1, P = 0.53; Cooper's Hawks: males = 13, females = 14, $\chi^2 = 0.04$, df = 1, P = 0.85), although the sex ratio of Cooper's Hawks differed between urban and rural habitats (urban: males = 2, females = 11; rural: males = 11, females = 3; Fisher exact test, P = 0.001). The age ratio was biased toward immatures in both species and was not significantly different between species (Sharp-shinned Hawks: adult = 14, immature = 26; Cooper's Hawks: adult = 11, immature = 16; $\chi^2 = 0.23$, df = 1, P = 0.63; Table 1).

Neither species nor sex were significant covariates of survivorship (log-likelihood χ^2 estimate = 1.98, df = 2, P = 0.37; sex: t <0.001, P > 0.99; species: t = 1.36, P = 0.17). Adult survival was significantly higher than juvenile survival (Mantel method, $\chi^2 = 4.42$, df = 1, P = 0.036). The probability of survival over the 110-day study period was 9.4% for juveniles and 75.4% for adults (Fig. 1). Mortality events occurred throughout the study up to 101 days after transmitter attachment; however, after the first 7 days, there was no evidence of increasing risk of mortality with time (Fig. 1). Although not significant, winter survival tended to be greater for Cooper's Hawks than for Sharp-shinned Hawks. Seven of 13 (53.8%) Cooper's Hawks with known fates survived the winter (i.e., itinerants and hawks with unknown fates removed from analysis), while only 8 of 23 (34.8%) Sharp-shinned Hawks survived (Table 1).

Many hawks appeared to be itinerant, as indicated by their lack of a stable home range (TCR and SLL unpubl. data) and eventual abandonment of the study site. Of the 27 Cooper's and 40 Sharp-shinned hawks captured, 5 (18.5%) and 11 (27.5%), respectively, left the study site (itinerants, Table 1). There was no significant effect of age on the tendency to be itinerant ($\chi^2 = 0.39$, df = 1, *P* = 0.53); on the three occasions when itinerant hawks left as they were being tracked, all moved south of the study site at least 20–30 km before we lost their signal.

As we tracked hawks through the end of winter, we recorded the proportion of individuals (of those with functioning transmitters) that remained on the study site during the

	Cooper's Hawk			Sharp-shinned Hawk		
	Adult	Immature	Total	Adult	Immature	Total
Total no. of hawks captured	11	16	27	14	26	40
Fate determined (54% of captured hawks) Died						
Collision	0	3	3	1	2	3
Predation	0	3	3	3	9	12
Survived						
Migrated	1	1	2	4	4	8
Resident	2	3	5			_
Total determined fates	3	10	13	8	15	23
% mortality of hawks with determined fate	0.0	60.0	46.2	50.0	73.3	65.2
Fate undetermined (46% of captured hawks)						
Itinerant	4	1	5	3	8	11
Unknown	4	5	9	3	3	6
Total undetermined fates	8	6	14	6	11	17

TABLE 1. Fates of wintering Cooper's and Sharp-shinned hawks captured in west-central Indiana, 1999–2004.

breeding season (Table 1). Sharp-shinned Hawks do not routinely breed in western Indiana, and all surviving Sharp-shinned Hawks (8/8) migrated north in late March or early April. Approximately 70% (5/7) of Cooper's Hawks were residents, while the remaining birds (2/7) were migrants. Of the migrant Cooper's Hawks, one died after a collision with a window about 75 km north of the study site.

Predation was a major source of mortality. Of all hawks (excluding itinerants and hawks

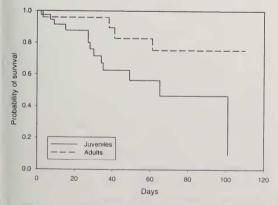


FIG. 1. Survivorship of wintering accipiters (Sharp-shinned and Cooper's hawks combined), by age class, in west-central Indiana, 1999–2004. Juvenile survival rate (solid line) is significantly lower than that for adults (dashed line; P = 0.036) based on the Cox proportional hazard model. See text for details.

with unknown fates), 23.1% (3/13) of Cooper's Hawks and 52.2% (12/23) of Sharpshinned Hawks were killed by a predator (Table 1). Of all causes of mortality, predation accounted for 50% (3/6) among Cooper's Hawks (two by owl and one by an unknown predator) and 80% (12/15) among Sharpshinned Hawks (six by owl, one by Cooper's Hawk, and five by unknown predators). This species-specific difference in predator-induced mortality was not significant (Fisher exact test, P = 0.29). Additionally, four hawks (three Sharp-shinned, one Cooper's) were depredated within 7 days of transmitter attachment (as noted above, these individuals were not included in the survivorship analysis). All predation on Cooper's Hawks occurred in the rural site; only accidental death was observed in the urban site.

Collisions with windows and automobiles were the main sources of accidental mortality. In the urban area, we documented two fatal collisions, one each with a window and an automobile. We also observed several non-lethal collisions with windows. In two cases, it seemed that hawks were attempting to attack a competitor (their reflection) and, as a result, hit the window first with their talons. The impact of such collisions did not seem to cause problems for the hawks during the course of the study. An additional urban hawk flew into an open garage, apparently suffered head injuries, and died 1 day later. In the rural area, we recorded two fatal collisions with windows—one with an automobile and one with a boulder, possibly during an attack. The latter event may have been an indirect effect of the recently attached transmitter (collision occurred 3 days after attachment).

DISCUSSION

The winter survivorship of Cooper's and Sharp-shinned hawks was approximately 9% for immatures and 75% for adults. Adult survival was significantly greater than that of immature hawks, but there was no significant effect of species or sex in the model. Mortality was caused predominantly by owl predation in the rural habitat and by accidents in the urban habitat.

The survival rates of adult Sharp-shinned and Cooper's hawks in our study fall within the range of those published elsewhere. Adult survivorship seems to be about 60-80% for most accipiters (Henny and Wight 1972, Boal 1997, Squires and Reynolds 1997, Tornberg and Colpaert 2001), and this is consistent with our results for the adults of both species. In addition, differences between juvenile and adult mortality have been observed in other accipiter populations such as Cooper's Hawks (Henny and Wight 1972, Boal 1997), Northern Goshawks (Kenward et al. 1999), and Sparrowhawks (Newton 1975; Newton et al. 1983, 1999). Although we also found age-related differences in accipiter mortality, juvenile survivorship (9.4%) in our study was lower than that typically reported for juvenile hawks elsewhere (20-50%; Henny and Wight 1972, Newton et al. 1983, Boal 1997, Kenward et al. 1999).

The high predation rates on juvenile hawks in our study might reflect a high site-specific abundance of owls, although we have no data on owl densities in our study area. Transmitter attachment also may have contributed to the low survival of juvenile hawks. We removed from our analyses four immature hawks that were depredated within the first 7 days of tracking, the period when we observed the greatest amount of excessive (>2 hr/day) transmitter grooming. Beyond this period, the survivorship functions of both adults and juveniles were generally linear. Given the potential difficulties experienced by juveniles in hunting and avoiding predators, the added mass, handling, and possible distraction by the transmitter attachment may have negatively influenced juvenile hawks. We note, however, that adult survival was not unusually low and no mortality was observed due to starvation. In addition, Reynolds et al. (2004) found no effect of backpack transmitters on goshawks, supporting the notion that our transmitters did not have a detrimental effect on survival. Whereas we used a synsacral mount rather than a backpack, the effects on flight dynamics are likely similar. Although we cannot separate predation on food-stressed or weakened hawks from predation on healthy hawks, we noted no emaciated birds among our recoveries. Furthermore, close inspection of all recaptured (one) or recovered (eight) hawks revealed no apparent long-term influence of transmitters or harnesses on the health of hawks, with the exception of one ectoparasite infestation localized under the transmitter (this bird was killed in an accidental collision). Overall, we suspect that juvenile survivorship in our study site was genuinely quite low.

Nearly 25% of our captured hawks were apparently itinerant. These hawks failed to maintain stable home ranges and typically disappeared within 14 days of capture. On three occasions, we managed to track itinerant hawks as they moved southward, and typically lost their signals 20-30 km south of the study site. This suggests that itinerant hawks were still moving southward, even as late as January. Furthermore, the Wabash River runs north-south through the study site and migrating hawks use geographical features such as rivers during migration (Zalles and Bildstein 2000); therefore, the presence of the river may have contributed to the proportion of migrating itinerants in our study site.

Our results indicate interesting differences in survivorship and causes of mortality between urban and rural habitats, but the lack of Sharp-shinned Hawks in urban habitats and relatively small numbers of rural Cooper's Hawks limited our ability to draw firm conclusions. Predation was common in the rural area, but was not observed in the urban area, which was consistent with Boal's (1997) observations. In our study, the lack of predation in the urban area may have been due to a lack

of owls and the numerical dominance of the larger female Cooper's Hawks (but see Mannan et al. 2004). In the absence of owls, large female hawks do not face the same mortality risks as their rural counterparts. In fact, our urban Cooper's Hawks were much more likely to hunt roosting prey at night by using the illumination of urban lighting and the moon. than were rural hawks (TCR and SLL pers. obs.). Rural hawks, particularly Sharp-shinned Hawks, may have avoided hunting in dim light due to the increased risk of predation from owls. Furthermore, the incidence of deadly collisions with windows and cars (one each) is surprisingly low in the urban habitat, given the concentration of such hazards in urban areas. Overall, our urban area is probably not a sink habitat for wintering Cooper's Hawks; however, some urban studies have revealed extremely high rates of mortality among urban Cooper's Hawks (particularly nestlings) during the breeding season (Boal 1997, Boal and Mannan 1999), suggesting that urban areas may sometimes represent reproductive sinks.

One might expect Sharp-shinned Hawks to occur frequently in the city given the large potential prey base (i.e., House Sparrows; Roth and Lima 2003) and a probable owl-free environment (TCR and SLL pers. obs.). However, we observed very few urban Sharpshinned Hawks. One possible explanation is that Sharp-shinned Hawks preferred the more dense vegetation typically found in our rural area. However, our rural Sharp-shinned Hawks frequently hunted in open areas such as near feeders and hedge rows where prey were abundant. Thus, we suggest that Sharpshinned Hawks avoided the urban habitat for other reasons: predation and possibly competition. The abundance of large female Cooper's Hawks in our urban habitat made it dangerous for all 100- to 400-g birds (Roth and Lima 2003), including Sharp-shinned Hawks (we had one apparent case of a Cooper's Hawk depredating a Sharp-shinned Hawk in our rural study area). Thus, the smaller Sharpshinned Hawk may have avoided the urban habitat due to a greater perceived risk of predation. In addition, urban Sharp-shinned Hawks may experience aggressive competition from Cooper's Hawks. Sharp-shinned Hawks frequently take larger prey, such as

starlings and Mourning Doves (*Zenaida macroura*; TCR and SLL unpubl. data), the main prey of urban Cooper's Hawks in our study area (Roth and Lima 2003).

Finally, our results suggest that future studies on the behavior of small wintering birds should consider the implications of intraguild predation in raptors. Owls are apparently a significant threat to rural hawks, especially Sharp-shinned Hawks, during the crepuscular periods. Thus, we would expect that rural hawks might reduce their activity during these periods unless food stressed. In fact, we observed a tendency for Sharp-shinned Hawks to leave roosts late (after sunrise) and return well before sunset (TCR and SLL unpubl. data; see also Sunde et al. 2003). Small birds may take advantage of periods when Sharpshinned Hawks are not active by feeding early and late in the day, and feed less during the midday when both Sharp-shinned and Cooper's hawks are active. In addition, Cooper's Hawks are a potential threat to Sharp-shinned Hawks during most of the day. Sharp-shinned Hawks may reduce their activity in areas where Cooper's Hawks are abundant (e.g., urban habitat), thereby reducing the risk of predation experienced by smaller birds, such as sparrows (Roth and Lima 2003).

ACKNOWLEDGMENTS

We thank W. E. Franklin, III, and our many field technicians for their assistance with hawk tracking. We also thank local businesses, landowners (especially M. Evrard, J. Irwin, C. Martin, and C. Miller), and the Terre Haute Parks Department for their cooperation. T. D. Steury provided insight into statistical analyses. C. E. Boal, J. Castrale, P. E. Scott, and two anonymous reviewers provided helpful comments on drafts of this manuscript. This research was supported, in part, by the National Science Foundation (Grant IBN–0130758), the Indiana Academy of Sciences, and the Indiana State University Department of Ecology and Organismal Biology and School of Graduate Studies.

LITERATURE CITED

- BERGER, D. D. AND H. C. MUELLER. 1959. The balchatri: a trap for the birds of prey. Bird-Banding 30:18–26.
- BILDSTEIN, K. L. AND K. MEYER. 2000. Sharp-shinned Hawk (Accipiter striatus). The Birds of North America, no. 482.
- BOAL, C. W. 1997. An urban environment as an ecological trap for Cooper's Hawks. Ph.D. dissertation, University of Arizona, Tucson.
- BOAL, C. W. AND R. W. MANNAN. 1999. Comparative

breeding ecology of Cooper's Hawks in urban and exurban areas of southeastern Arizona. Journal of Wildlife Management 63:77–84.

- BOAL, C. W., R. W. MANNAN, AND K. S. HUDELSON. 1998. Trichomoniasis in Cooper's Hawks from Arizona. Journal of Wildlife Diseases 34:590– 593.
- BOINSKI, S. AND P. A. GARBER. 2000. On the move: how and why animals travel in groups. University of Chicago Press, Chicago, Illinois.
- Cox, D. R. 1972. Regression models and life-tables. Journal of the Royal Statistical Society, Series B 34:187–220.
- DEWEY, S. R. AND P. L. KENNEDY. 2001. Effects of supplemental food on parental-care strategies and juvenile survival of Northern Goshawks. Auk 118:352–365.
- GEORGE, J. R. 1989. Bald Eagle kills Sharp-Shinned Hawk. Journal of Raptor Research 23:55–56.
- HENNY, C. J. AND H. M. WIGHT. 1972. Population ecology and environmental pollution: Red-tailed and Cooper's hawk. Pages 229–250 in Population ecology of migratory birds: a symposium. Wildlife Research Report, no. 2. U.S. Fish and Wildlife Service, Washington, D.C.
- HOUSTON, A. AND J. MCNAMARA. 1999. Models of adaptive behavior. Cambridge University Press, Cambridge, United Kingdom.
- HOUSTON, C. S., D. G. SMITH, AND C. ROHNER. 1998. Great Horned Owl (*Bubo virginianus*). The Birds of North America, no. 372.
- KAPLAN, E. L. AND P. MEIER. 1958. Nonparametric estimation from incomplete observations. Journal of American Statistical Association 53:457–481.
- KENWARD, R. E., V. MARCSTROM, AND M. KARLBOM. 1999. Demographic estimates from radio-tagging: models of age-specific survival and breeding in the Goshawk. Journal of Animal Ecology 68: 1020–1033.
- KERAN, D. 1981. The incidence of man-caused and natural mortalities to raptors. Raptor Research 15: 108–112.
- KLEM, D., JR. 1990. Collisions between birds and windows: mortality and prevention. Journal of Field Ornithology 61:120–128.
- KLEM, D., JR., B. S. HILLEGASS, AND D. A. PETERS. 1985. Raptors killing raptors. Wilson Bulletin 97: 230–231.
- KLEM, D., JR., D. C. KECK, K. L. MARTY, A. J. MILLER BALL, E. E. NICIU, AND C. T. PLATT. 2004. Effects of window angling, feeder placement, and scavengers on avian mortality at plate glass. Wilson Bulletin 116:69–73.
- LEHMAN, R. N. 2001. Raptor electrocution on power lines: current issues and outlook. Wildlife Society Bulletin 29:804–813.
- LIMA, S. L. 1985. Maximizing feeding efficiency and minimizing time exposed to predators: a trade-off in the Black-capped Chickadee. Oecologia 66:60– 67.
- MANGEL, M. AND C. W. CLARK. 1988. Dynamic modeling in behavioral ecology. Princeton University Press, Princeton, New Jersey.

- MANNAN, R. W., W. A. ESTES, AND W. J. MATTER. 2004. Movements and survival of fledgling Cooper's Hawks in an urban environment. Journal of Raptor Research 38:26–34.
- MAZUR, K. M. AND P. C. JAMES. 2000. Barred Owl (*Strix varia*). The Birds of North America, no. 508.
- NEWTON, I. 1975. Movements and mortality of British Sparrowhawks. Bird Study 22:35–43.
- NEWTON, I., M. MARQUISS, AND P. ROTHERY. 1983. Age structure and survival in a Sparrowhawk population. Journal of Animal Ecology 52:591–602.
- NEWTON, I., I. WYLLIE, AND L. DALE. 1999. Trends in number and mortality patterns of Sparrowhawks (Accipiter nisus) and Kestrels (Falco tinnunculus) in Britain, as revealed by carcass analyses. Journal of Zoology 248:139–147.
- PALMER, R. S. 1988. Handbook of North American birds, vol. 4. Yale University Press, New Haven, Connecticut.
- PULLIAM, H. R. AND T. CARACO. 1984. Living in groups: is there an optimal group size? Pages 127–147 in Behavioral ecology: an evolutionary approach, 2nd. ed. (J. R. Krebs and N. B. Davies, Eds.). Blackwell Press, Oxford, United Kingdom.
- RAPPOLE, J. H. AND A. R. TIPTON. 1994. New harness design for attachment of radio transmitters to small passerines. Journal of Field Ornithology 62: 335–337.
- REYNOLDS, R. T., G. C. WHITE, S. M. JOY, AND R. W. MANNAN. 2004. Effects of radiotransmitters on Northern Goshawks: do tailmounts lower survival of breeding males? Journal of Wildlife Management 68:25–32.
- ROSENFIELD, R. N. AND J. BIELEFELDT. 1993. Cooper's Hawk (Accipiter cooperii). The Birds of North America, no. 75.
- ROTH, T. C., II, AND S. L. LIMA. 2003. Hunting behavior and diet of Cooper's Hawks: an urban view of the small-bird-in-winter paradigm. Condor 105: 474–483.
- SPSS INSTITUTE, INC. 1998. SYSTAT for Windows, ver. 10.0. SPSS Institute, Inc., Chicago, Illinois.
- SQUIRES, J. R. AND R. T. REYNOLDS. 1997. Northern Goshawk (Accipiter gentilis). The Birds of North America, no. 298.
- STEPHENS, D. W. AND J. R. KREBS. 1986. Foraging theory. Princeton University Press, Princeton, New Jersey.
- SUNDE, P., M. S. BOLSTAD, AND K. B. DESFOR. 2003. Diurnal exposure as a risk sensitive behavior in Tawny Owl (*Strix aluco*). Journal of Avian Biology 34:409–418.
- TORNBERG, R. AND A. COLPAERT. 2001. Survival, ranging, habitat choice, and diet of the Northern Goshawk *Accipiter gentilis* during winter in northern Finland. Ibis 143:41–50.
- WARD, J. M. AND P. L. KENNEDY. 1996. Effects of supplemental food on size and survival of juvenile Northern Goshawks. Auk 113:200–208.
- ZALLES, J. I. AND K. L. BILDSTEIN (EDS.). 2000. Raptor watch: a global directory of raptor migration sites. BirdLife Conservation Series, no. 9. BirdLife International, Cambridge, United Kingdom.